TWO NEW SPECIES OF *GRATIOLA* (PLANTAGINACEAE) FROM EASTERN NORTH AMERICA AND AN UPDATED CIRCUMSCRIPTION FOR *GRATIOLA NEGLECTA*

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ABSTRACT

Gratiola section *Nibora*, a North American taxon as currently circumscribed, includes six species: *G. ebracteata*, *G. flava*, *G. floridana*, *G. heterosepala*, *G. neglecta*, and *G. virginiana*. *Gratiola ebracteata* and *G. heterosepala* are restricted to western North America and the remaining four species are mostly eastern North American. The species with the largest range and greatest degree of morphological variability is *G. neglecta*. A recent investigation of *G. neglecta* involving fieldwork, examination of herbarium specimens, morphological analysis, and phytogeographic study, has resulted in the discovery of two undescribed species, **G. graniticola** sp. nov. and **G. quartermaniae** sp. nov., both of which are endemic to rock outcrop communities of eastern North America. In this paper, both new species are described, illustrated, and compared to their widespread congener, *G. neglecta*. An updated circumscription of *G. neglecta* is provided and a key distinguishing the new species from *G. neglecta* is included.

RESUMEN

Gratiola sección *Nibora*, un taxon norteamericano como se circumscribe normalmente, incluye seis especies: *G. ebracteata*, *G. flava*, *G. floridana*, *G. heterosepala*, *G. neglecta*, y *G. virginiana*. *Gratiola ebracteata* y *G. heterosepala* están restringidas al oeste de Norte América y las restantes cuatro especies están principalmente en el este de Norte América. La especie con el rango más amplio y el mayor grado de variabilidad morfológica es *G. neglecta*. Una investigación reciente de *G. neglecta* con trabajo de campo, examen de especimenes de herbario, análisis morfológico, y estudio fitogeográfico, ha dado como resultado el descubrimiento de dos nuevas especies, **G. graniticola** sp. nov. y **G. quartermaniae** sp. nov., ambas endémicas de comunidades de afloramientos rocosos del este de Norte América. En este artículo, se describen e ilustran ambas especies, y se compraran con su congénere generalizada *G. neglecta*. Se aporta una circunscripción puesta al día de *G. neglecta* y se incluye una clave para diferenciar las nuevas especies de *G. neglecta*.

Gratiola L. section *Nibora* (Raf.) Pennell (Plantagianceae) was erected by Pennell (1935) to accommodate the annual North American species characterized by having capsules equaling or slightly exceeding the sepals, leaves sessile to scarcely clasping and obscurely glandular punctate, and seeds yellowish and faintly reticulate. Pennell (1935) recognized five species within the section: *G. ebracteata* Benth., *G. flava* Leavenw., *G. floridana* Nutt., *G. neglecta* Torr., and *G. virginiana* L. Mason and Bacigalupi (1954) added a sixth species to this section when they described *G. heterosepala* Mason & Bacig. from northern California. *Gratiola ebracteata* and *G. heterosepala* are restricted to western North America while *G. flava*, *G. floridana*, and *G. virginiana* are mostly eastern North American (*G. virginiana* is also disjunct to central Mexico). *Gratiola neglecta* is the most widespread and most variable species in the section, ranging across much of temperate North America. Throughout its broad range, *G. neglecta* inhabits a wide diversity of wetland communities and exhibits considerable variation in degree of branching, stem pubescence, leaf shape, flower morphology, and capsule size.

Recent evidence from field and herbarium studies indicates that material previously referred to *G. neglecta* includes two undescribed species. The first new species, *G. quartermaniae* D. Estes sp. nov., has a highly fragmented distribution in eastern North America and is endemic to ephemerally wet sites associated with calcareous outcrops (cedar glades) and prairies. The second new species, *G. graniticola* D. Estes sp. nov., is endemic to north-central Georgia where it is restricted to vernal pools on granitic outcrops. In this paper, both new species are described, illustrated, and compared to their widespread congener, *G. neglecta*. Because *G. quartermaniae* and *G. graniticola* have been included within the concept of *G. neglecta* by previous authors, an updated circumscription of *G. neglecta* is provided.

J. Bot. Res. Inst. Texas 1(1): 149 – 170. 2007

MATERIALS AND METHODS

In order to clarify morphological variation within and between *G. neglecta*, *G. quartermaniae*, and *G. graniticola*, an investigation was conducted that incorporated fieldwork, examination of herbarium specimens, morphological analyses, and phytogeography. Fieldwork was conducted in portions of 26 states in the United States and the province of Ontario, Canada between 2001 and 2006. In addition, more than 4,000 herbarium specimens (including some digital images), representing all taxa from sect. *Nibora,* were examined from the following 49 herbaria: A, ALU, APSC, ASTC, AUA, BRIT, CAN, CITA, CLEMS, DAO, DUKE, EKY, FSU, GA, GH, H, ILLS, ISC, JEPS, JSU, K, KANU, LL, LSU, MIN, MISS, MO, MTSU, NCSC, NCU, NLU, NO, NY, NYS, OKL, PH, SBSC, SMU, TENN, TEX, TROY, TRT, UARK, UC, UNA, US, USCH, VDB, and VPI (herbarium acronyms follow Index Herbariorum, http://www.nybg.org/bsci/ih/search).

From the herbarium specimens examined during this project, a subset of 87 mature and complete specimens representing 55 *G. neglecta*, 15 *G. graniticola*, and 17 *G. quartermaniae*, was selected for use in a morphometric study. Specimens were chosen to represent the full geographic distribution, range of habitat, and morphological variation of each species. For each specimen, 10 quantitative vegetative and floral characters were measured (Table 1); these specimens are denoted by an asterisk in the lists of representative specimens examined. Seed measurements were taken from five of the above specimens (1 *G. graniticola*, 4 *G. neglecta)* plus an additional 14 specimens representing a total of 10 widespread populations of *G. neglecta*, four of *G. graniticola*, and five of *G. quartermaniae.* Twenty seeds from a single capsule were measured per population, and three quantitative characters were scored per seed (Table 1). Specimens used for seed measurements are indicated by a dagger (†) in the lists of specimens examined. For each scored character, summary statistics including mean, standard deviation, and range were calculated; these values are presented in Table 1. In the taxonomic key and species descriptions, measurements for characters are given as the mean ± one standard deviation with extreme values, based on additional observations, given in parentheses. In order to reveal discontinuities in the data and to determine which characters are most useful for delimiting taxa, pairwise comparisons of characters were conducted using scatter diagrams and box plots. Seeds and trichomes of all three species were also examined with the aid of scanning electron microscopy (SEM) to search for useful taxonomic characters. The geographic distribution of *G. neglecta, G. graniticola,* and *G. quartermaniae* was determined by examining the collection data included on herbarium specimens and plotting the county-level distribution of each species on outline maps. Each point on these maps is represented by at least one herbarium specimen examined.

RESULTS AND DISCUSSION

Morphology

Gratiola neglecta, G. quartermaniae, and *G. graniticola* form a morphologically cohesive group referred to here as the *Gratiola neglecta* complex. A fourth species, *G. floridana*, also belongs to this complex; however, it is quite distinct morphologically in spite of sharing a suite of features uniting it with the other three species. *Gratiola floridana* differs from the other members of the complex in its overall larger features including much larger flowers 13–25 mm long (vs. 5–14 mm), longer proximal fruiting pedicels averaging 23–43 mm long (vs. 12–25 mm), and longer seeds averaging 0.79–0.9 mm (vs. 0.4–0.6 mm). This species tends to inhabit forested sites whereas the others mostly grow in open communities. It is also the southernmost member of the complex ranging from northwestern Florida and southeastern Louisiana (historically) north into southeastern Tennessee. The distribution of *G. floridana* only slightly overlaps with the ranges of *G. neglecta* and *G. quartermaniae* in the northern portion of its range. Since *G. floridana* is one of the most distinctive species of the genus and has rarely been confused with *G. neglecta* or the two new species, it will not be discussed further.

Several characters distinguish *G. graniticola* from *G. neglecta* and *G. quartermaniae* (Table 2; Fig. 1, Fig. 2). *Gratiola graniticola* has shorter leaves (normal leaves that subtend pedicels are also referred to as bracts or bracteal leaves in this paper) that are widest at or below the middle (Fig. 2 A), shorter pedicels that

Table 1. Morphological characters measured for *Gratiola graniticola*, *G. neglecta*, and *G. quartermaniae* and their means ± standard deviations and ranges (parentheses). *N*=sample size.

Characters	***G. graniticola* (N=15)**	***G. neglecta* (N=55)**	***G. quartermaniae* (N=17)**
Stem height (cm)	14.8 ± 5.9 (7.4–29.4)	19.9 ± 5.5 (10.2–33.2)	16.5 ± 5.1 (5.8–29)
Stem diameter (mm)	1.2 ± 0.2 (0.7–1.4)	1.6 ± 0.5 (0.8–2.9)	1.4 ± 0.4 (0.6–2.3)
Leaf length (mm)	10 ± 2.8 (6.3–17.7)	30.8 ± 10.3 (11–66)	25.1 ± 7.0 (16–43)
Leaf width (mm)	2.1 ± 1.0 (1.1–5.2)	7.7 ± 2.6 (2.7–18)	3.3 ± 0.8 (1.8–4.5)
Leaf length/leaf width (ratio)	4.6 ± 1.0 (2.8–7.45)	4.1 ± 0.80 (2.6–6.1)	7.7 ± 1.8 (5.5–11.2)
No. teeth per leaf margin	1.0 ± 0.7 (0–3)	3.5 ± 1.2 (1–7)	1.2 ± 1.1 (0–3)
Proximal pedicel length (mm)	12.4 ± 4.9 (5.3–22)	20.6 ± 7.7 (10.5–37)	17 ± 4.2 (8–22)
Bract length (mm)	8.7 ± 2.2 (5.3–11.2)	28.8 ± 9.5 (11.5–66)	21.8 ± 6.6 (12.5–33)
Pedicel length/bract length (ratio)	1.5 ± 0.4 (0.9–2.3)	0.8 ± 0.3 (0.3–1.3)	0.8 ± 0.3 (0.5–1.6)
Capsule length (mm)	3.2 ± 0.3 (2.9–3.6)	4.3 ± 0.6 (2.6–5.7)	4.1 ± 0.6 (3.4–5.1)
	***G. graniticola* (N=80)**	***G. neglecta* (N=200)**	***G. quartermaniae* (N=100)**
Seed length (mm)	0.40 ± 0.03 (0.31–0.47)	0.54 ± 0.06 (0.42–0.7)	0.59 ± 0.04 (0.43–0.71)
Seed diameter (mm)	0.22 ± 0.02 (0.17–0.27)	0.24 ± 0.02 (0.18–0.29)	0.29 ± 0.03 (0.19–0.37)
Seed length/seed width (ratio)	1.86 ± 0.24 (1.32–2.53)	2.3 ± 0.27 (1.67–3.03)	2.05 ± 0.27 (1.47–2.6)

are longer relative to their subtending bracts (Fig. 2, D–E), smaller corollas that have a purplish or pinkish posterior lobe and beard of whitish trichomes, bracteoles that are shorter than to only slightly exceeding the calyces, smaller more subglobose purple-tinged capsules (Fig. 2 F), smaller seeds (Fig. 2 G–H; Fig. 3 A), and bulbous-based trichomes (Fig. 3). *Gratiola neglecta* and *G. quartermaniae* have longer leaves (Fig. 2 A), longer pedicels that are mostly equal to or shorter than their subtending bracts (Fig 2, D–E), larger corollas that usually lack purplish or pinkish coloration and that have a beard of yellow trichomes inside the corolla orifice, bracteoles that are mostly longer than the calyces, larger more ovoid and brownish capsules (Fig. 2 F), larger seeds (Fig. 2, G–H; Fig. 3 B–C), and slender-based trichomes (Fig. 3, E–F). A scatter diagram of leaf length vs. capsule length between *G. graniticola*, *G. neglecta*, and *G. quartermaniae* reveals two primary clusters that exhibit minimal overlap (Fig. 1 A). In this scatter plot, specimens of *G. graniticola* mostly group separately from the second unresolved cluster that consists of specimens of *G. neglecta* and *G. quartermaniae*. A scatter plot of proximal pedicel length/subtending bract length vs. leaf width also distinguishes *G. graniticola* from *G. neglecta* (Fig. 1 B).

Gratiola quartermaniae differs from *G. neglecta* in having a glabrous midstem, narrower (Fig. 2 B) and more falcate, fewer veined and fewer toothed leaves that have a larger length to width ratio (Fig. 2 C) and seeds that average longer, thicker, and darker (Fig. 2, G–H). In comparison to *G. quartermaniae*, *G. neglecta* has mostly pubescent (rarely glabrate in some New England estuarine populations) midstems, wider (Fig. 2 B), more veined and more toothed leaves that have a smaller leaf length to width ratio (Fig. 2 C). The seeds

Table 2. Qualitative morphological characters useful for distinguishing *G. graniticola*, *G. neglecta*, and *G. quartermaniae*.

Character	*G. graniticola*	*G. neglecta*	*G. quartermaniae*
Stems	simple–rarely branched	branched–rarely simple	simple–rarely branched
Leaf shape	lanceolate-ovate to narrowly oblong	narrowly elliptic, rhombic, or oblanceolate	linear, linear-lanceolate, or elliptic-lanceolate
Basal leaf disposition	± congested	not congested	± congested
Widest point of leaf	middle or below middle	middle or beyond middle	middle
Proximal bract to pedicel ratio	bract < pedicel	bract ≥ pedicel	bract ≥ pedicel
Mid-stem vestiture	glandular-pubescent	glandular-pubescent	glabrous
Trichome shape	bulbous-based	slender-based	slender-based
Ratio bracteole length/calyx length	bracteoles ≤ to slightly exceeding calyx	bracteoles ≥ calyx	bracteoles ≥ calyx
Posterior corolla lobe color	purplish or pinkish	white (rarely pinkish)	white (rarely pinkish)
Beard color	white	yellow	yellow
Capsule shape	subglobose	ovoid	ovoid
Capsule color	purplish	brown	brown
Seed color	grayish-brown	yellowish-brown	grayish-brown
Habitat	granite outcrops	various wetland types, rarely on outcrops	limestone/dolomite outcrops, calcareous prairies

of *G. neglecta* are lighter in color and average slightly shorter and are not as thick as those of *G. quartermaniae* (Fig. 2, G–H). In Fig. 1 C, a scatter plot of leaf length/leaf width vs. number of teeth per margin for *G. neglecta* and *G. quartermaniae* reveals two clusters of specimens.

Distribution and Ecology

Gratiola neglecta has the largest distribution of the three species, being found throughout most of temperate North America (Fig. 4). It ranges from Nova Scotia and British Columbia, Canada, south in the United States to central Georgia, coastal Texas, northern Arizona, and northern California. The species is most common in the eastern United States particularly in the lower Mississippi, Missouri, and Ohio River valleys. West of the Mississippi River, the range of *G. neglecta* mostly follows the major river systems toward the Great Plains. From the upper Missouri River watershed, *G. neglecta* ranges south into the southern Rocky, Cascade, and Sierra Nevada mountains. Several populations in the western United States are associated with reservoirs; these may represent recent introductions by migrating waterfowl. Interestingly, *G. neglecta* has also been collected in France (*Simon s.n.* FSU; *Rastetter 11653* UC) and Finland (*Lampinen 5629* H; see Suominen 1984) where probably introduced.

Gratiola neglecta grows in a broader array of wetland communities and endures a greater range of environmental conditions than *G. graniticola* or *G. quartermaniae*. It grows from sea level to an elevation of 2400 m in the mountains of the western United States. Compared to the new species, *G. neglecta* occurs more frequently in the deeper soil of agricultural fields, openings in bottomland hardwood forests, wet meadows, mudflats, and pond margins. Rarely, *G. neglecta* occurs in salt marshes or on various types of shallow-soiled rock outcrops including igneous, sandstone, limestone, and granite formations.

Gratiola quartermaniae has a fragmented range (Fig. 5) and is most common in the limestone cedar glades of the Interior Low Plateau of middle Tennessee and northern Alabama. From this core range, it is disjunct to the alvars of southeastern Ontario, Canada, a distance of ca. 1200 km. Most of the Ontario populations are associated with the Napanee limestone plain but a few are found in the Dummer Moraine and Prince Edward Peninsula physiographic regions (Chapman & Putnam 1984). Numerous other species that are more common on calcareous outcrops in the southeastern United States also occur on Canadian alvars including several of the species commonly associated with *G. quartermaniae* in Tennessee and Alabama such as *Carex granularis* Muhl. ex Willd., *C. crawei* Dewey, *C. molesta* Mack. ex Bright, *Isanthus brachiatus* (L.)

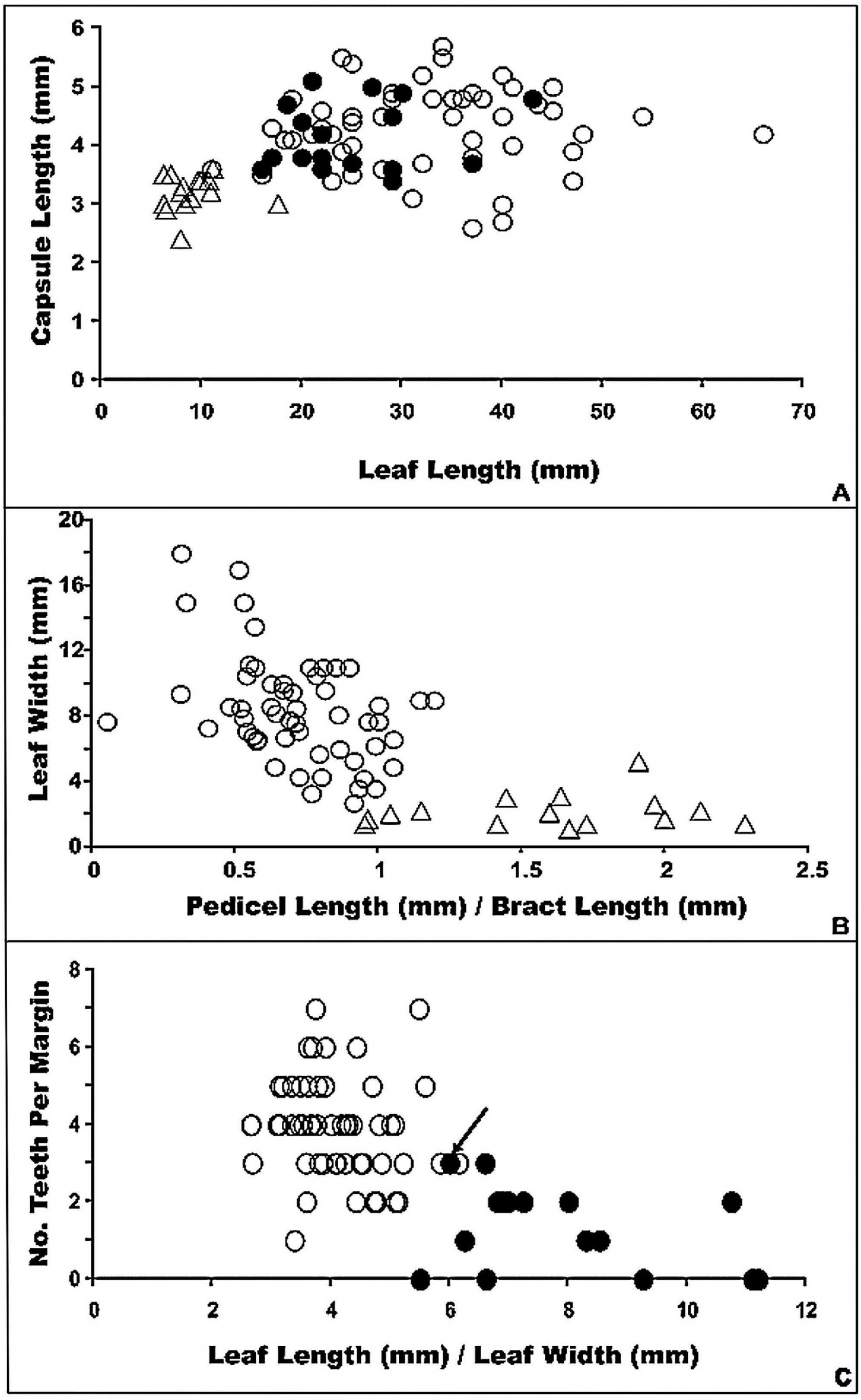

FIG. 1. Scatter plots of leaf length vs. capsule length (A), proximal pedicel length/subtending bract length vs. leaf width (B), leaf length/leaf width vs. number of teeth per margin (C) for *G. graniticola* (open triangles), *G. neglecta* (open circles), and/or *G. quartermaniae* (closed circles). Note that open circles in panel C represent specimens with pubescent mid-stems, and solid circles represent plants with glabrous mid-stems with one exception; the solid circle marked with an arrow has features typical of *G. quartermaniae* except for having a pubescent mid-stem. This specimen (*Kral 52812*, VDB, Cannon Co., TN) was collected from a seep over limestone at the edge of the range of *G. quartermaniae* and may represent a hybrid.

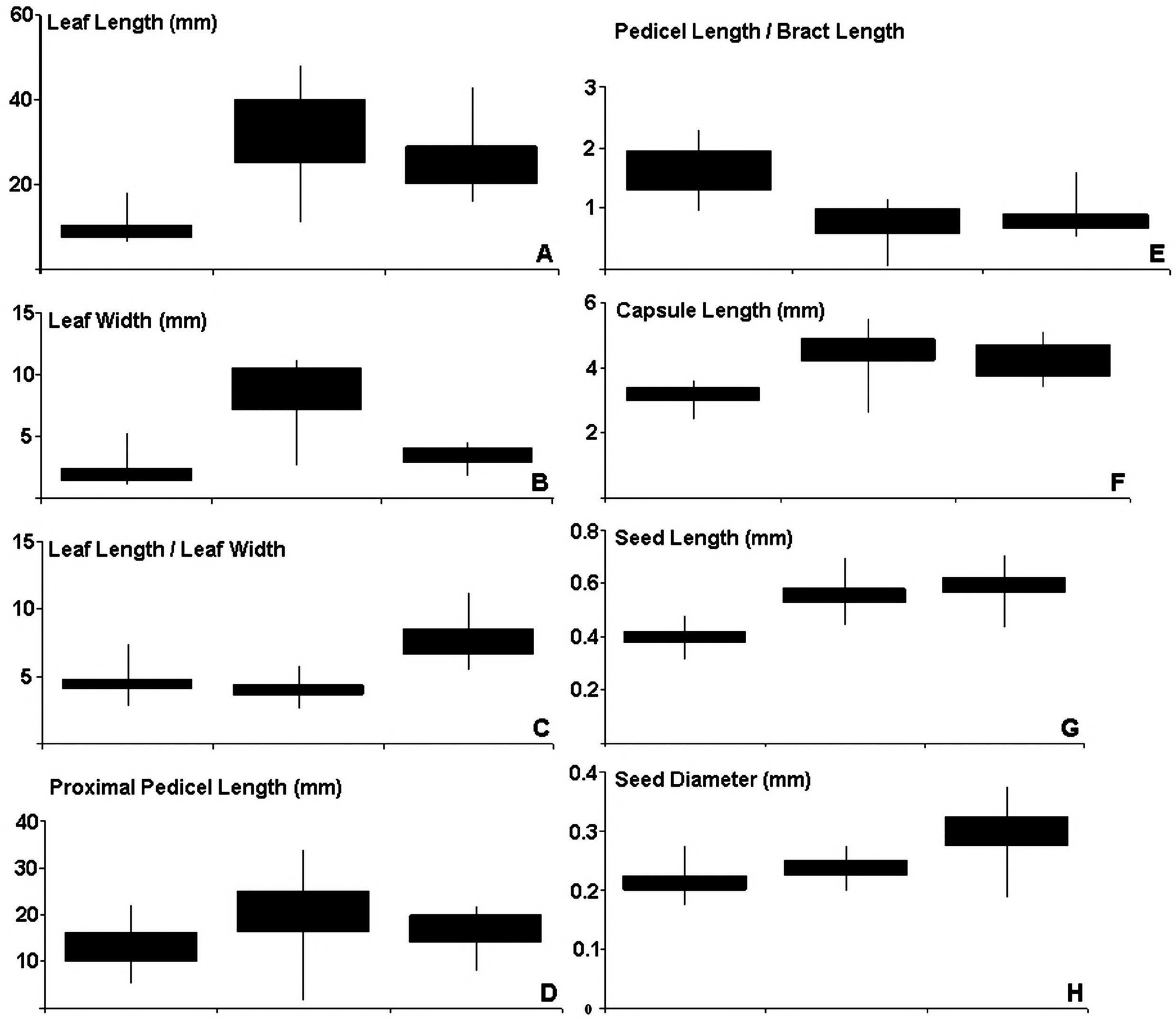

Fig. 2. Graphical comparison of eight selected characters for *Gratiola graniticola* (left), *G. neglecta* (center), and *G. quartermaniae* (right): leaf length (A), leaf width (B), ratio of leaf length to leaf width (C), proximal pedicel length (D), ratio of proximal pedicel length to subtending bract length (E), capsule length (F), seed length (G), and seed diameter (H).

B.S.P., *Scutellaria parvula* Michx., and *Sporobolus vaginiflorus* (Torr. ex Gray) Wood. *Gratiola quartermaniae* is also disjunct to Will County, Illinois from its main range in central Tennessee, a distance of approx. 600 km. Two limestone glade near-endemics, *Dalea foliosa* (Gray) Barneby and *Astragalus tennesseensis* Gray ex Chapman, share this similar distribution pattern (Baskin & Baskin 2003). *Gratiola quartermaniae* is also disjunct to the Edward's Plateau of Texas, a distance of ca. 1200 km. Interestingly, *Juncus filipendulus* Buckley, a species that *G. quartermaniae* frequently occurs with in Alabama and Tennessee, is also disjunct to the Edward's Plateau where it occurs with *G. quartermaniae*. Therefore, while the disjunction patterns exhibited by *G. quartermaniae* are unusual, further examination indicates that in each of these areas *G. quartermaniae* occurs in similar habitat and always occurs with other calciphilous species, some of which have similar patterns of disjunction. This species should be searched for in other regions where calcareous outcrops and prairies occur such as the limestone glades of the southern Ridge and Valley of southeastern Tennessee and northwestern Georgia, the Blackbelt prairies of Mississippi and Alabama, the limestone glades of central and western Kentucky, the Ozark glades of southern Missouri and northern Arkansas, and alvar habitats in New York, Michigan, and Ohio.

Gratiola quartermaniae is found on limestone or dolomite outcrops and calcareous prairies. In these

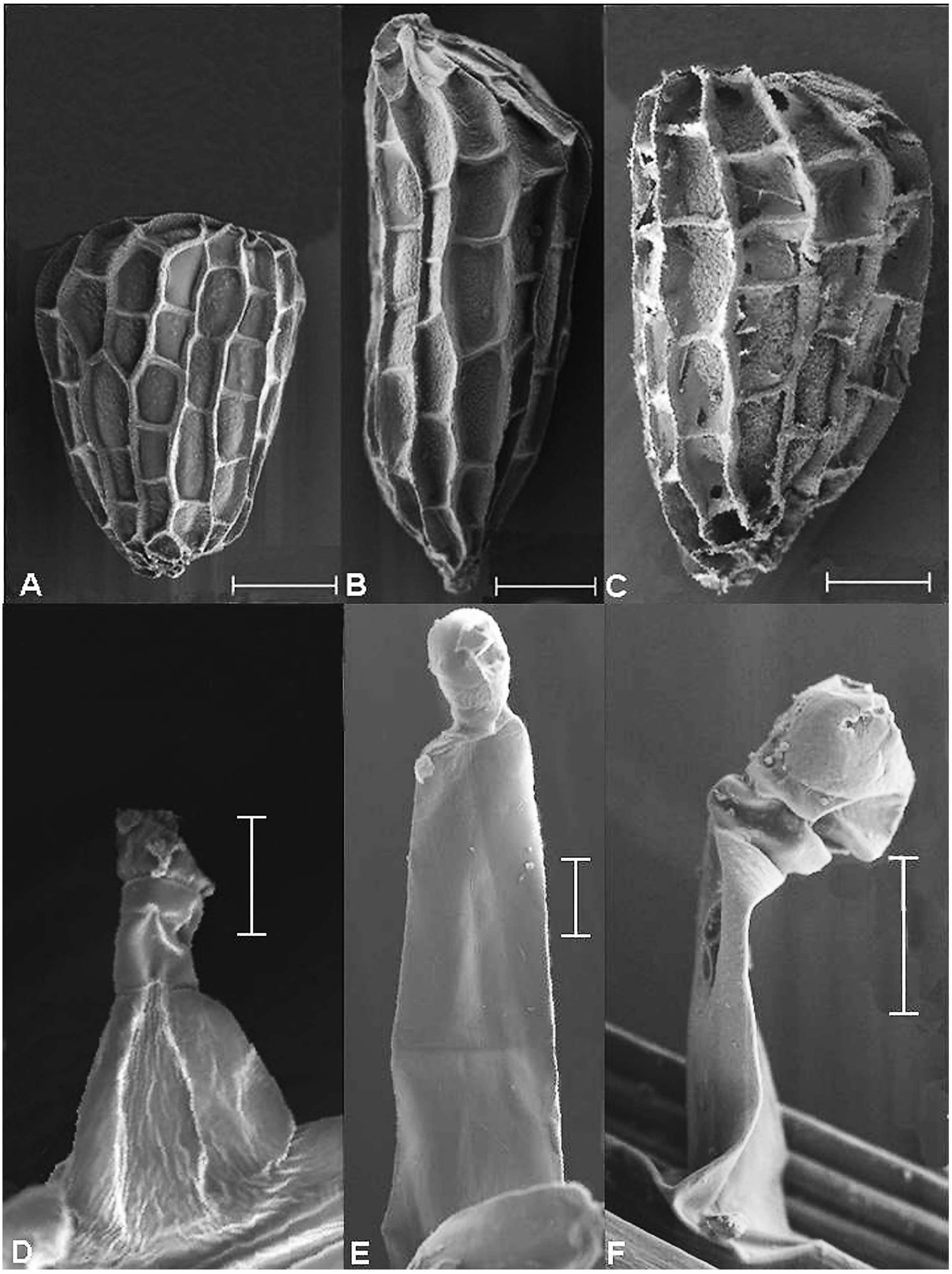

Fig. 3. Seeds of *Gratiola graniticola* (A), *G. neglecta* (B), and *G. quartermaniae* (C); scale bars = 100 µm. Trichomes of *G. graniticola* (D), *G. neglecta* (E), and *G. quartermaniae* (F); scale bars = 20 µm.

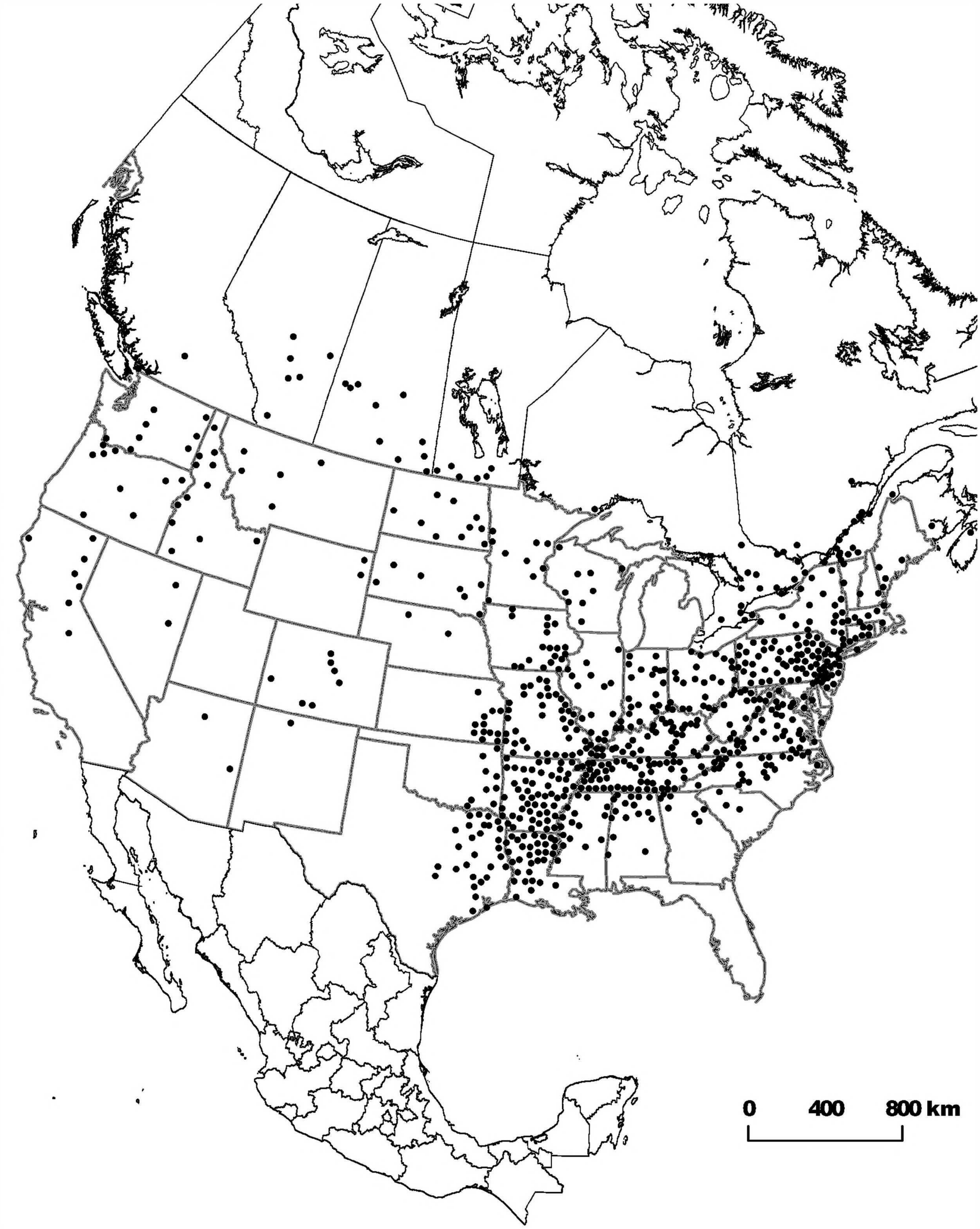

Fig. 4. Geographic distribution of *Gratiola neglecta* in North America.

habitats, the species predominantly occurs in shallow clayey soils of ephemeral pools, seasonal streambeds, and periodically wet meadows on or immediately adjacent to outcrops. These sites are usually flat to slightly sloping and are located in areas that receive high to moderate levels of sunlight. They are wet in late winter

Fig. 5. Geographic distribution of *Gratiola quartermaniae*.

and early spring but become severely desiccated by late spring and early summer. Rarely, *G. quartermaniae* occurs in situations otherwise more typical for *G. neglecta* such as low wet fields, open wet woods, and marsh edges, but these populations are always located within close proximity to glade habitat. Limestone glade endemics such as *Leavenworthia alabamica* Rollins, *L. crassa* Rollins, *L. torulosa* Gray, and *Lesquerella lyrata*

Rollins are sometimes found in disturbed non-outcrop habitats often in association with *G. quartermaniae*. In central Tennessee and northern Alabama, *G. quartermaniae* is almost always associated with limestone cedar glade endemics or calciphiles such as *Allium cernuum* Roth, *Carex crawei*, *C. granularis*, *Dalea foliosa*, *D. gattingeri* (Heller) Barneby, *Eleocharis bifida* S.G. Smith, *Hypericum sphaerocarpum* Michx., *Isoetes butleri* Engelm., *Juncus filipendulus*, *Leavenworthia* spp., *Ludwigia microcarpa* Michx., *Mecardonia acuminata* (Walt.) Small, *Sedum pulchellum* Michx., *Sporobolus vaginiflorus*, and *Talinum calcaricum* Ware. In areas where *G. quartemaniae* is disjunct as in Ontario, Illinois, and Texas, the species is associated with a number of additional calciphilous taxa, including a few of those listed above.

Gratiola graniticola is restricted to granite outcrops in 13 counties on the Piedmont Plateau of Georgia (Fig. 6). Of the approx. 17 Piedmont granite outcrop endemics (McVaugh 1943; Weakley 2007), *G. graniticola* is one of only five species, along with *Isoetes melanospora* Engelmann, *I. piedmontana* (N.E. Pfeiffer) C.F. Reed, *I. tegetiformans* Rury, and *Amphianthus pusillus* Torr., restricted to the ephemeral pools of the outcrops. Interestingly, *I. tegetiformans* and *G. graniticola* are the only Piedmont granite outcrop endemics completely restricted to Georgia.

All known populations of *G. graniticola* occur on granite outcrops in water-filled depressions lined with a thin layer of soil. These depressions are filled with water during the winter and spring months but dry out in the summer and fall. Species commonly associated with *G. graniticola* include *Croton willdenowii* G.L. Webster, *Cyperus granitophilus* McVaugh, *Diamorpha smallii* Britt. ex Small, *Eleocharis obtusa* (Willd.) Schult., *Isoetes piedmontana* (N.E. Pfeiffer) C.F. Reed, *Juncus georgianus* Coville, *Lindernia monticola* Muhl. ex Nutt., *Minuartia uniflora* (Walt.) Mattf., *Packera tomentosa* (Michx.) C. Jeffrey, *Pilularia americana* A.Braun, *Rhynchospora* sp., and *Schoenolirion croceum* (Michx.) A. Gray.

Gratiola quartermaniae is sympatric with *G. neglecta*; however, the two species generally occupy different habitat types. They occur syntopically at a few sites in middle Tennessee and northern Alabama where the typical glade habitat of *G. quartermaniae* occurs in close proximity to habitats preferred by *G. neglecta*. Each of these sites is located within ca. 500 m of a cedar glade or glade-like area. Plants at these sites appeared to belong either to *G. quartermaniae* or to *G. neglecta* with no obvious hybrids observed at most sites. One specimen (*Kral 52812* VDB, MO) collected from a seep over limestone in Cannon County, Tennessee appears to be typical *G. quartermaniae* in general morphology and habitat; however, the middle portion of the stems on this specimen are slightly pubescent and more typical of *G. neglecta* (Fig. 1 C). It is possible that this specimen represents a hybrid between *G. neglecta* and *G. quartermaniae*. Although *G. neglecta* was not found on any cedar glades in middle Tennessee or northern Alabama, the species has been collected from a variety of rock outcrop types elsewhere where it exhibits morphological features typical of non-outcrop populations. *Gratiola floridana* is sympatric with both *G. quartermaniae* and *G. neglecta* in northern Alabama's Moulton Valley (Lawrence and Morgan counties). Although these three species have been found within 1 km of each other, sites supporting all three species are unknown. *Gratiola floridana* and *G. quartermaniae* occur syntopically at one site in Lawrence County, Alabama (*Whetstone et al. 16471* JSU, mixed collection of *G. floridana* and *G. quartermaniae*). *Gratiola floridana* usually inhabits shaded muddy sites in forested bottoms or ravines but in northern Alabama it rarely occurs in habitats more typical of *G. quartermaniae*. No obvious hybrids between *G. floridana* and *G. quartermaniae* or between *G. floridana* and *G. neglecta* have been discovered.

The range of *G. graniticola* lies near the southern edge of the range of *G. neglecta* and the two species overlap only in northeastern Georgia (Elbert and Greene counties). Although the Greene County specimen of *G. neglecta* (*Allison 2630* GA) was collected from a granite outcrop, the two species have never been observed growing syntopically and no putative hybrids have been found. A disjunct population of *G. graniticola* reportedly occurs on a granite outcrop in Lancaster County, South Carolina (J. Allison, Georgia Natural Heritage Program, pers. comm.), but specimens needed to confirm this report have not been located.

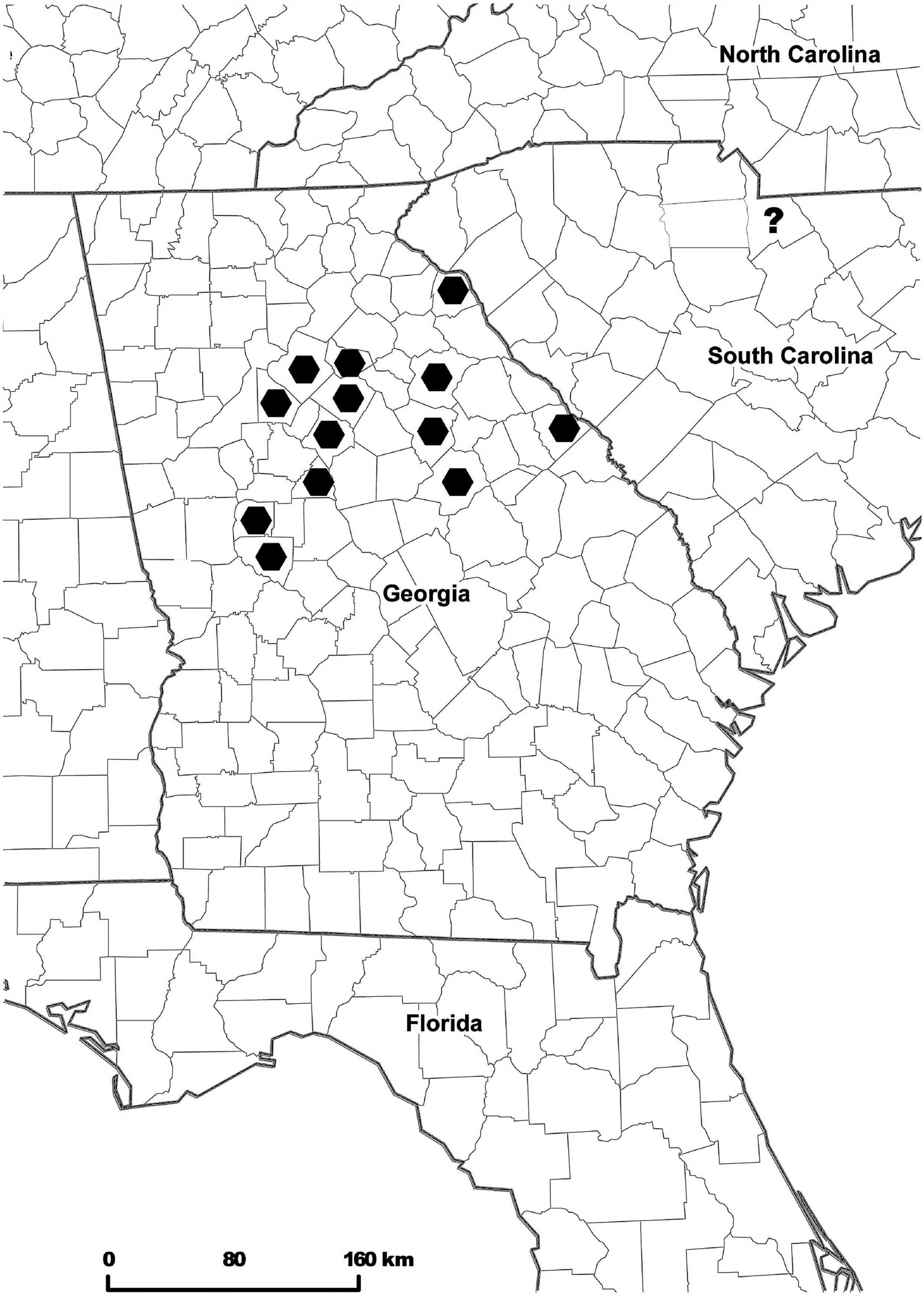

Fig. 6. Geographic distribution of *Gratiola graniticola*. The question mark represents an unconfirmed report from Lancaster Co., South Carolina.

KEY TO THE SPECIES OF THE *GRATIOLA NEGLECTA* COMPLEX

1. Flowers 13–25 mm long, adaxial surface of the corolla lobes pilose; proximal fruiting pedicels (20–)23–43(–55) mm long; seeds (0.6–)0.79–0.9 mm long, trichomes short stalked, the stalks approximately equaling or shorter than the glandular head _____ **G. floridana**
1. Flowers 5–14 mm long, adaxial surface of the corolla lobes glabrous; proximal fruiting pedicels (5–)12–25(–37) mm long; seeds (0.3–)0.4–0.6(–0.7) mm long, trichome stalks ≥ 1.5 times as long as the glandular head.
   2. Mid-stem leaves (11–)20–41(–66) mm long; proximal fruiting pedicels (8–)13–25(–37) mm long, (0.3–)0.5–1(–1.6) times as long as the subtending bracteal leaves; bracteoles slightly longer to conspicuously longer than the sepals; posterior corolla lobe white (rarely inconspicuously tinged with pink or lavender); beard inside corolla orifice of yellow trichomes; mature capsules ovoid, brown; seeds (0.4–)0.5–0.6(–0.7) mm long and (0.18–)0.21–0.29(–0.37) mm thick, trichomes slender-based.
      3. Leaves narrowly elliptic or rhombic to oblanceolate, not conspicuously falcate, (2.7–)5–11(–18) mm wide at widest point; length to width ratio (2.5–)3.5–5(–6), each margin with (1–)3–5(–7) often conspicuous teeth, primary veins 3–5 (7); mid-stem moderately to densely glandular pubescent (rarely glabrate), seeds (0.18–)0.22–0.26(–0.29) mm thick _____ **G. neglecta**
      3. Leaves linear, linear-lanceolate, to elliptic-lanceolate, often falcate, (1–)2.5–4(–4.5) mm wide at widest point, length to width ratio (5.5–)6–9.5(–11), entire or each margin with 1–2(–3) inconspicuous teeth, primary vein 1(–3); mid-stem glabrous, seeds (0.19–)0.26–0.32(–0.37) mm thick _____ **G. quartermaniae**
   2. Mid-stem leaves (6–)7–13(–18) mm long; proximal fruiting pedicels (5–)7–17(–22) mm long, (0.9–)1–2(–2.3) times as long as the subtending bracteal leaves; bracteoles shorter than to barely exceeding sepals; posterior corolla lobe conspicuously tinged with pink or purple; beard inside corolla orifice of white trichomes; mature capsules subglobose, purplish; seeds (0.3–)0.36–0.42(–0.5) mm long and (0.17–)0.20–0.24(–0.27) mm thick, trichomes bulbous based _____ **G. graniticola**

TAXONOMIC TREATMENT

Gratiola neglecta Torr,, Catal. Pl. New York. 10, 89. 1819. (**Fig. 7**). TYPE: [no locality data on specimen, but as noted by Stuckey (1979) this specimen was donated to the Schweinitz herbarium by John Torrey. Torrey (1819) gives the locality as "Inundated and moist places, New York."], [no collection date provided on sheet or in Torrey (1819)], [collector not specified on sheet but Pennell (1935) noted "it is almost certainly a plant of Torrey's collecting…"]. (LECTOTYPE, here designated: PH!; ISOLECTOTYPE, here designated: K-digital image!).

Conobea borealis Spreng., Neue Entdeck 3:26. 1822.

Gratiola missouriana Beck, Amer. Jour. Sci. 10:258. 1826.

Gratiola odorata Raf., Autik. Bot. 43. 1840.

Gratiola heterophylla Raf., Autik. Bot. 43. 1840.

Gratiola gracilis Benth., Prod. Syst. Nat. Regn. Veg. 10:402. 1846.

Gratiola officinalis Michx. *ß caroliniensis* Pers., Syn. Plant. 1:14. 1850.

Gratiola lutea Raf. var. *glaberrima* Fernald, Rhodora 34:149. 1932. *Gratiola neglecta* Torr. var. *glaberrima* (Fernald) Fernald, Rhodora 51:84. 1949.

Plants annual, solitary, erect herbs, (10–)16–27(–33) cm tall. Roots simple, fleshy, whitish with numerous rootlets. Stems erect, somewhat fleshy, simple or with few to many spreading-ascending branches, terete or slightly rounded-quadrangular in cross section, (0.8–)1.2–2.2(–2.9) mm in diameter at midstem; with (6–)7–10(–12) leafy nodes, mid-stem internodes (17–)28–45(–48) mm long, basal internodes not conspicuously shortened; stem green, usually densely short glandular-pubescent from below middle to apex, becoming glabrate near the base or rarely glabrate throughout, trichomes spreading, translucent, slender-based and gland-tipped. Leaves simple, oppositely-decussate, narrowly elliptic or rhombic to oblanceolate, or uncommonly falcate, spreading, 3–5(–7)-veined, thin, mid-cauline blades (11–)24–44(–66) mm long and (3–)5–11(–18) mm wide, (2.5–)3.5–5(–6) times longer than wide, median leaves usually largest decreasing in size toward base and apex, apex acute, widest at or just distal to the midpoint, margins with (1–)2–5(–7) remotely spaced low and inconspicuous to sharp and evident teeth per margin, base acuminate and sessile or slightly clasping; blades green, glabrate to moderately glandular pubescent. Flowers solitary in axils of upper median and distal bracteal leaves, erect to spreading, zygomorphic, perfect; pedicels slender, ascending to divergent, (10–)12–30(–37) cm long, (0.27–)0.44–0.94(–1.33) times as long as the bracteal leaves, densely to sparsely pubescent with slender-based gland-tipped trichomes. Bracteoles 2, paired, closely subtending

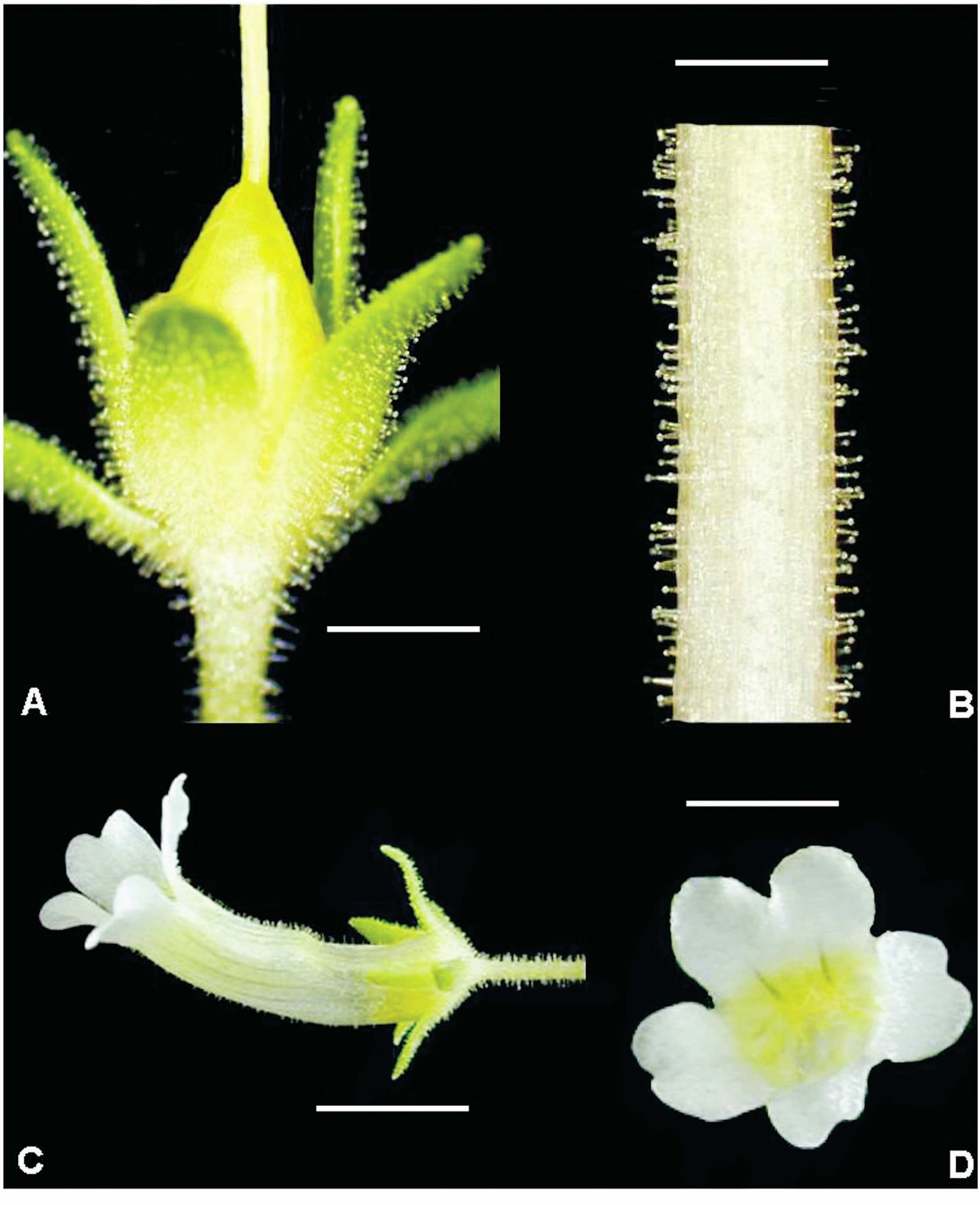

Fig. 7. *Gratiola neglecta*. A. Flowering calyx (corolla removed) and bracteoles (scale bar = 2 mm). B. Close-up of mid-stem (scale bar = 2 mm). C. Flower, lateral view (scale bar = 4 mm). D. Flower, front view (scale bar = 2.5 mm).

the calyx, lanceolate, narrowly elliptic, to oblanceolate, sometimes falcate, apex narrowly obtuse to acute, margins with 1–2 inconspicuous teeth, bases straight or tapering, longitudinally 3-nerved, in flower 2.5–7 mm long and 0.5–1 mm wide, enlarging as fruit matures and becoming foliose and up to 15 mm long and 2 mm wide, thin, green or minutely purple-tipped, sparsely to densely covered with slender-based gland-

tipped trichomes on both surfaces. Calyx irregularly campanulate with 5 subequal sepals; these distinct, lanceolate, longitudinally 3-veined, slightly fleshy, green, (2.2–)3–4.4(–5) mm long and ca. 0.5 mm wide, apex narrowly obtuse, margins entire, sparsely to densely covered with gland-tipped trichomes. Corolla tubular, gamopetalous, zygomorphic, slightly marcescent, 6.5–12 mm long; corolla tube quadrangular, dorsal surface with a prominent hump near midpoint, the ventral surface canaliculate, to 9 mm long, to 2.1 mm in diameter proximal to dorsal hump, pale yellow, yellowish-cream, or yellowish-green, with many dichotomously forking brownish-violet lines extending from the tube base to the base of the corolla lobes, sparsely to moderately glandular pubescent pubescent externally with slender gland-tipped trichomes, inner surface near orifice at base of posterior corolla lobe with moderate to dense beard of clavately thickened yellow trichomes, proximal and median inner corolla tube pilose with eglandular trichomes; corolla lobes 5, generally slightly broader than high and obtuse to emarginated, spreading, white, 1.7–2.5 mm long and 3.2–3.8 mm wide; the posterior lobe generally largest, the two lateral lobes and lower lobe equal or slightly smaller, adaxial surfaces glabrous, abaxial surfaces glabrous or slightly glandular pubescent. Stamens 2, inserted near the middle of dorsal surface of the corolla tube, filaments to 1.2 mm long, anthers transversely oriented to the filaments, 0.6–0.8 mm long and 0.4–0.6 mm wide, connective greatly dilated around the two anther sacs, whitish; staminodes inserted ca. 1.5 mm above base of corolla or absent, when present ca. 0.3 mm long and not capitate. Gynoecium 5.3–6.8 mm long, subtended at the base by an orange nectary ring, ovary 1.4–3.3 mm long and to 2.1 mm in diameter, style 3.0–3.9 mm, stigma 2-lobed, dilated and flattened, ca. 0.7 mm long. Capsules ovoid, apex acute to obtuse, usually widest below the middle, (2.6–)3.6–5(–6) mm long, 3–5 mm in diameter, brown at maturity. Seeds several hundred per capsule, brownish-yellow, 10–13 ribbed, longitudinal ridges more conspicuous than the transverse ridges, asymmetrically ovoid to cylindric, often oblique at one end, reticulate with rectangular alveolae, alveolae covered by a thin iridescent membrane, (0.42–)0.48–0.60(–0.70) mm long and (0.18–)0.22–0.26(–0.29) mm in diameter, (1.7–)2–2.6(–3) times longer than wide. Chromosome number: 2N=18 (Gervais et al. 1999).

Phenology.—Flowering and fruiting from March to October

Common Name.—Clammy hedge-hyssop

Specimens Measured.—**CANADA. ONTARIO:** Thunder Bay District, 8 km SW of Thunder Bay City, 17 Aug 1978, *Garton 18549* (ISC*). **QUEBEC: Montmorency Co.:** Ange-Gardien, 23 Jul 1963, *Cinq-Mers et al. 69-169* (UC*). **Portneuf Co.:** Portneuf, 7 Jul 1941, *Rouleau 1045* (PH*). **SASKATCHEWAN**: 8 mi E of Saskatoon, 6 Jul 1950, *Ledginham 890* (SMU*).

U.S.A. ALABAMA: Greene Co.: Smith Lake (swamp) ca. 14 mi due WNW of Eutaw, 1 May 1980, *Haynes 7775* (UNA*). **Limestone Co.:** Beaverdam Creek 0.01 mi N of US Hwy 72 / Alt. 20 bridge, Wheeler Wildlife Refuge, 20 May 1980, *Meigs 555* (UNA*). **ARIZONA. Apache Co.:** River Reservoir, Greer Lakes, 1.4 mi E of AZ Hwy 373, 2 airmi NE of Greer, and 9 airmi W of Eagar, 30 Aug 1988, *Ricketson & Raechal 4415* (MO*). **ARKANSAS. Union Co.:** El Dorado, 3 May 1940, *Demaree 22048* (PH*†). **CONNECTICUT. Hartford Co.:** Suffield, 20 Jun 1923, *Weatherby s.n.* (NCSC*). **DELAWARE. New Castle Co.:** 0.5 mi W of Glasgow, 15 Jun 1929, *Benner 3572* (PH*). **GEORGIA. Bartow Co.:** Big Belfry Pond, 4.8 mi E of Adairsville, 5 May 1951, *Duncan 12316* (US*). **Walker Co.:** Chickamauga, 16 May 1900, *Biltmore 3913a* (US*). **ILLINOIS. Johnson Co.:** Ferne Clyffe State Park; floodplain of Buck Branch, 21 May 1992, *Mibb 692* (NLU*). **McHenry Co.:** McHenry, 15 Jun 1925, *Benke 4083* (US*). **INDIANA. Vanderburgh Co.:** 0.5 mi S of Staser, 26 May 1926, *Deam 42953* (PH*). **KANSAS. Cherokee Co.:** 0.5 mi W of Crestline, 6 Jun 1970, *Magrath 5352* (VDB*†). **Greenwood Co.:** T28S, R13E, sec 9, edge of temporary pool of valley in scrub oak woodland, 13 May 1987, *McGregor 38094* (GA*). **KENTUCKY. Warren Co.:** along Warren Co. Rt. 1288, ca. 1 mi from intersection with Warren Co. 961, 5 Jun 1968, *Nicely 1666* (NCSC*). **LOUISIANA. Richland Parish:** beside S side of I-20E ca. 1.7 mi W of the Rayville Exit (La. 137), 8 May 1990, *Thomas 115,966* (TENN†). **MASSACHUSETTS. Berkshire Co.:** Mount Washington, 25 Aug 1923, *Meredith s.n.* (PH*). **Worcester Co.:** Boylston, 24 Jun 1962, *Richardson s.n.* (MO*). **MINNESOTA. Carlton Co.:** between Holyoke and Foxboro, 4 Jul 1942, *Lakela 4986* (SMU*). **MISSISSIPPI. Carroll Co.:** field beside MS 7, at Avalon, 17 May 1973, *Thomas & Marx 34783* (SMU*†). **Washington Co.:** ca. 3.5 mi NE Leland, 12 May 1988, *Bryson 7637* (VPI*). **MISSOURI. Pulaski Co.:** Falls Hollow Sandstone Glade, Ft. Leonard Wood, 13 May 1994, *Hays 434* (MO*). **MONTANA. Lake Co.:** 4 mi S and 2 mi W of Ronan, 8 Jul 1956, *Harvey 6517* (NCU*). **NEVADA. Elko Co.:** 0.8 road mi E of Deeth on the road to O'Neil Basin, backwaters of the Marys River, 4 Jul 1986, *Tiehm 10727* (BRIT*). **NEW JERSEY. Cumberland Co.:** Maurice River W of Bricksboro, 3 Jun 1934, *Long 43311* (PH*). **NEW MEXICO. Rio Arriba Co.:** vicinity of Chama, 9 Jul 1911, *Standley 6659* (US*). **NEW YORK. Clinton Co.:** Rouses Point, 7 Aug 1910, *Williamson s.n.* (PH*). **Monroe Co.:** near Rochester, 4 Jul 1913, *Baxter s.n.* (MO*). **NORTH CAROLINA. Cabarrus Co.:** Rocky River at NC Rd. 73, 25 May 1969, *Daggy 5478* (TENN†). **Caswell Co.:** by Hyco Creek SE of Hightowers, 22 May 1958, *Bell 11947* (NCU*). **Chatham Co.:** 3 mi W of Mann's Chapel on Co. Rd. 1536, 22 May 1974, *Massey & Levesque 3988* (NCU*). **NORTH DAKOTA. Cass Co.:** Harwood, 30 Jun 1937, *Stevens 246* (GA*); 7 mi W of Enderlin, 28 Aug 1968, *Barker 5213* (MO†). **Richland Co.:**

Wyndmere, 18 Jun 1965, *Stevens 2775* (US*). **OHIO. Champaign Co.:** Thackery, 11 Jun 1914, *Leonard s.n.* (US*). **Crawford Co.:** ca. 1.5 mi NW of Lykens, 30 Sep 1979, *Stuckey 9962* (PH*). **Erie Co.:** W of Ceylon, Berlin Township, 15 Jul 1973, *Jones 73-7-15-802* (TENN†). **OKLAHOMA**. **Le Flore Co.:** along Poteau River, near Howe, 25 May 1931, *Palmer 39340* (MO*). **McCurtain Co.:** near Harris, ca. 2 mi N of the Red River, 20 Apr 1946, *Nelson, Nelson, & Goodman 5579* (TEX*). **OREGON. Crook Co.:** Farewell Bend, 17 Jul 1894, *Leiberg 456* (US*). **PENNSYLVANIA. Chester Co.:** French Creek near Hallman, 25 Jun 1927, *Stone s.n.* (PH*). **SOUTH DAKOTA. Brookings Co.:** T112N R52W S32 SW4 SW4, restored prairie pothole wetland, 15 Jul 1991, *Galatowitsch s.n.* (ISC*). **Custer Co.:** Custer, 25 Jul 1892, *Rydberg 924* (US*). **TENNESSEE. Gibson Co.:** floodplain of North Fork of Forked Deer River near jct. with Hwy 104, 6 Jul 1979, *Boom, Whitten, and Wofford 529* (TENN†). **Giles Co.:** NW side of Ardmore, N of Hwy 7 along N side of Austin Witt Rd. E of intersection of Austin Witt Rd. and Union Hill Church Rd., 5 May 2001, *Estes 02059* (TENN*). **Hardin Co.:** side of Pittsburgh Landing Rd., S of Walker Branch, 18 May 1989, *Guthrie & Tennesen 2235* (NCU*). **Weakley Co.:** E side of TN 89 along floodplain of Cane Creek, ca. 1.5 mi N of Palmerville, 25 May 1981, *Webb 3919a* (VDB*). **TEXAS. Franklin Co.:** 3 mi E of Mount Vernon, off US 67, 3 May 1945, *Lundell 13701* (LL*). **Jasper Co.:** 9.3 mi NE of Burkeville, 14 Apr 1960, *Shinners 27909* (SMU*). **VIRGINIA. Giles Co.:** Flat Top Mtn. near the upper end of Pearis Thompson Branch, NE of Holly Brook, 7 Aug 1990, *Wieboldt 7368* (NCU*). **Warren Co.:** Waterlick, 19 Jun 1924, *Pennell 12113* (US*). **WASHINGTON. Klickitat Co.:** Lyle, small shoal in Columbia River on the east side of the mouth of the Klickitat River, 26 Aug 1993, *Halse 4697* (K*). **Spokane Co.:** margin of Newman Lake, 2 Jul 1927, *St. John 8811* (MO*). **Whitman Co.:** wet pond beds, Pullman, 1 Aug 1896, *Elmer 163* (US†). **WEST VIRGINIA. Tucker Co.:** 0.25 mi S of Burley's Camp, Cabin Mtn. Range, 8 Jul 1941, *Allard 9055* (US*†). **Wetzel Co.:** near Littleton, 1 Jul 1961, *Haught 7127* (BRIT*). **WISCONSIN. Lincoln Co.:** Tomahawk Twp., 18 Jul 1950, *Seymour 11687* (MO*). **Taylor Co.:** near Rib River, 22 Jun 1957, *Schlising 648* (UC*).

Gratiola quartermaniae D. Estes, sp. nov. (**Fig. 8**). TYPE: CANADA. ONTARIO. Hastings Co.: Tyendinaga Township, "Toddary" alvar, Daley Road, ca. 7.5 km N of Lonsdale, 44.3404 N, 77.14539 W, moist open areas on alvar, with *Eleocharis compressa, Rumex crispus, Eleocharis obtusa,* 22 Jun 2006, *Oldham, Norris, & Van Sleeuwen 32809* (HOLOTYPE: TENN; ISOTYPES: BRIT, CAN, DAO, NHIC, NY, MO).

Gratiola quartermaniae a *G. neglecta* Torr. differt herba magis sparsim pubescente; caulibus plerumque simplicibus vel infrequenter ramosis, ad medium glabris; foliis angustioribus falcatis, lineari-lanceolatis vel elliptico-lanceolatis, marginibus integris vel inconspicue dentata, laminis plerumque uni- vel trinervis; seminis parum longioribus crassioribusque, magis fusce brunneis.

Plants annual, solitary, erect herbs, (6–)11–22(–30) cm tall. Roots simple, fleshy, whitish with numerous rootlets. Stems erect, fleshy, simple or with few ascending branches, terete or slightly rounded-quadrangular in cross section, (0.6–)1–1.9(–2.3) mm in diameter at midstem; with 7–10(–11) leafy nodes, mid-stem internodes (12–)19–35(–38) mm long, basal internodes shortened, 1–7 mm long; green or suffused with reddish or reddish-pink pigments, especially near the base or upper nodes; glabrous or nearly so from the base to above the middle, becoming sparsely glandular pubescent among the upper flower-bearing nodes with spreading, translucent, slender-based gland-tipped trichomes. Leaves simple, oppositely-decussate, similar in shape but gradually reduced in size from base to apex, lowermost often congested due to the shortened internodes and sometimes early deciduous, linear, linear-lanceolate to elliptic-lanceolate, often falcate, spreading or ascending, mostly with one evident main vein, sometimes trinerved with two short secondary veins, rarely the two secondary veins well-developed, slightly fleshy-thickened, mid-cauline blades (16–)18–32(–43) mm long and (1–)2.5–4(–4.5) mm wide, (5.5–)6–9.5(–11) times longer than wide, apex acute or narrowly obtuse, widest near the middle, base sessile or slightly clasping; margins entire or each margin with 1–2(–3) remote, low, bluntly pointed teeth beyond the middle; blades green, the basal blades sometimes suffused with red; glabrous or nearly so. Flowers solitary in the axils of middle and upper bracteal leaves, erect to spreading, zygomorphic, perfect; pedicels slender, ascending to divergent, (8–)13–22 mm long, 0.5–1.1(–1.6) times as long as the subtending bracteal leaves, sparsely pubescent with slender-based gland-tipped trichomes. Bracteoles 2, paired, closely subtending the calyx, equaling or to 2.3 times longer than the sepals, linear-oblanceolate to linear-lanceolate and often falcate, one-nerved or inconspicuously trinerved with two small lateral nerves, in fresh material bracteoles often appearing nerveless, fleshy-thickened, in flower 2.8–8.2 mm long, lengthening in fruit to 11.8 mm long, 0.7–1.0 mm wide, apex obtuse, margins entire, surface green, sparsely to moderately covered with slender-based gland-tipped trichomes. Calyx irregularly campanulate with 5 subequal, distinct, lanceolate sepals, each inconspicuously longitudinally three-nerved, in fresh material appearing single-nerved or apparently nerveless, fleshy-thickened, green, 2.7–5.1 mm long and 0.7–1.0 mm wide, apex obtuse, margins entire, sparsely covered with slender-based gland-tipped trichomes. Corolla tubular-funnelform, gamopetalous, zygomorphic, slightly marcescent,

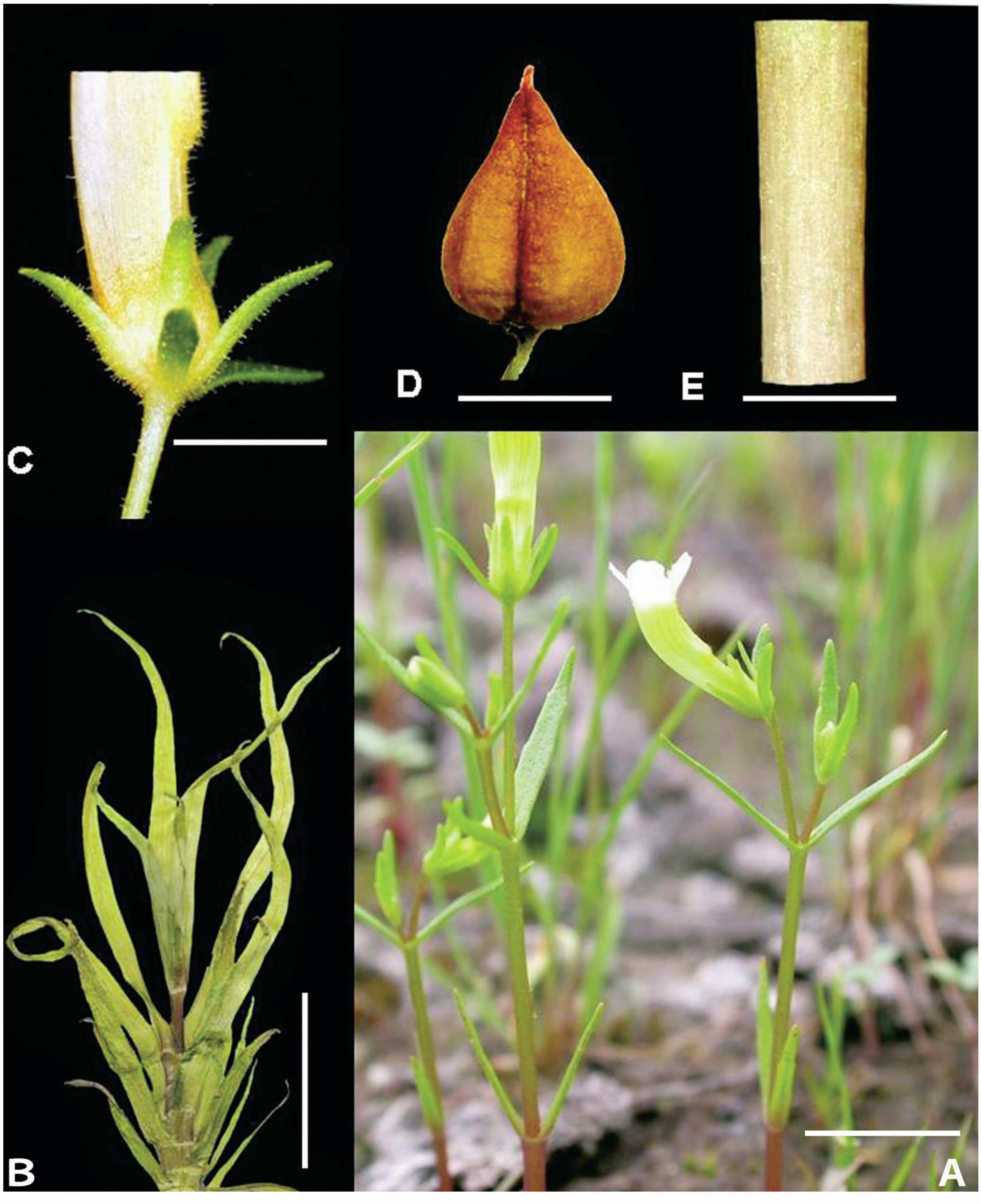

Fig. 8. ***Gratiola quartermaniae*****. A. Habit of** ***G. quartermaniae*** **at type locality (photo by M. Oldham, 2 Jun 2006). B. Pre-flowering specimen showing congested basal leaves (pressed specimen from** ***D. Estes 04359*** **TENN; scale bar = 2 cm). C. Flowering calyx and bracteoles (scale bar = 4 mm). D. Capsule (from** ***Oldham et al. 32877*** **TENN; scale bar = 3.5 mm). E. Close-up of mid-stem (scale bar = 2 mm).**

6–13.7 mm long; corolla tube quadrangular, dorsal surface with a prominent hump near midpoint, the ventral surface canaliculate, to 9.3 mm long, 1.3–2.7 mm in diameter proximal to dorsal hump, greenish-yellow, creamy yellow, or bright yellow, with many brownish-purple lines extending the length of the tube,

sparsely pubescent externally with slender-based gland-tipped trichomes, inner surface near orifice at base of posterior corolla lobe with moderate to dense beard of clavately thickened yellow trichomes, proximal and median inner corolla surfaces pilose with eglandular trichomes up to 0.8 mm long; corolla lobes 5, generally slightly broader than high and emarginate, white, 2.0–3.6 mm long and 2.4–5.4 mm wide; the posterior lobe generally largest, the two lateral lobes and lower lobe equal or slightly smaller, adaxial surfaces glabrous, abaxial surfaces glabrous or slightly glandular pubescent. Stamens 2, inserted near the middle of the dorsal surface of the corolla tube, filaments 0.8–1.5 mm long, anthers transversely oriented to the filaments, 0.8–1.3 mm long and 0.5–0.9 mm wide, connective whitish and greatly dilated around the two anther sacs; staminodes inserted 1.4–1.8 mm above base of corolla or absent, when present to 0.3 mm long, not capitate. Gynoecium 5.9–7.6 mm long, subtended at the base by an orange nectary disc, ovary 1.6–4.3 mm long and 1–2.8 mm in diameter, style 3.1–4.6 mm, stigma 2-lobed, dilated and flattened, 0.6–0.9 mm long. Capsules ovoid, apex acute, usually widest below the middle, (3.4–)3.6–4.7(–5.1) mm long, 2.9–4.5 mm in diameter, brown at maturity. Seeds several hundred per capsule, grayish-brown to reddish-brown, 10–13 ribbed, longitudinal ridges more conspicuous than the transverse ridges, asymmetrically ovoid to oblong-cylindric, often oblique at one end, reticulate with rectangular alveolae, alveolae covered by a thin iridescent membrane, (0.43–)0.55–0.63(–0.71) mm long and (0.19–)0.26–0.32(–0.37) mm in diameter, (1.5–)1.8–2.3(–2.6) times longer than wide. Chromosome number unknown.

Phenology.—Flowering and fruiting from April to early June in Alabama, Tennessee, Texas and from June to August in Illinois and Ontario, Canada

Etymology.—This species is named in honor of Dr. Elsie Quarterman, retired Vanderbilt University plant ecologist, who has dedicated her career to the study of the ecology of the limestone cedar glades and the species that inhabit them.

Common Name.—Quarterman's hedge-hyssop; limestone hedge-hyssop.

Conservation Status.—*Gratiola quartermaniae* is most common in the limestone cedar glades of middle Tennessee where it is known from ca. 30 populations in nine counties. Although it appears to be secure in Tennessee, the mid-state area where this species occurs is one of the most rapidly developing regions in the southeastern U.S. and the once abundant glade habitat preferred by this species is increasingly being destroyed. Consequently, while *G. quartermaniae* is not sufficiently rare in Tennessee now to warrant state or federal conservation status, its populations should be monitored in the next few decades. In Alabama, Illinois, Texas, and Ontario this species appears to be quite rare and is restricted to small geographic areas. In these regions it should be afforded protection at the state or provincial level.

Representative Specimens.—**CANADA. ONTARIO. Hastings Co.:** Belleville, May 1861, *Macoun* [number illegible] (K); vicinity of Belleville, Jun 1867, *Macoun 17454* (CAN*); flats near the Iron Bridge at Belleville, Jun 1868, *Macoun 41730* (CAN); Belleville, 10 Jun 1871, *Macoun 123* (TRT); Belleville, 24 Jun 1871, *Macoun 1261* (DAO); Pt. Anne, Belleville, Ontario, 13 Jun 1972, *Morton 5091* (CAN, QK, TRT, WAT); Hungerford Township, Larkins Alvar, ca. 9.5 km SE of Tweed, ca. 1.5 km SW of Larkins, S of Marlbank Rd., 30 Jun 2006, *Oldham, Norris, & Van Sleeuwen 32877* (DAO, MICH, MO, NHIC, TENN, US); Richmond Township, Roblin Dump alvar, ca. 1.5 km SE of Roblin, ca. 9 km SSE of Marlbank, 30 Jun 2006, *Oldham, Norris, Sutherland & Van Sleeuwen 32869* (CAN, MICH, MO, NHIC, NY, TENN, TRTE, US, UWO). **Lennox and Addington Co.:** Camden East Township, ca. 10 km NW of Newburgh, ca. 15 km N of Napanee, road to Roblin Hell Holes, off Centreville Road, 30 Jun 2006, *Oldham 32868* (BRIT, CAN, DAO, HAM, MICH, MO, MT, NHIC, TENN, US, VDB). **Peterborough Co.:** alvar ca. 2 mi N of Nogies Creek in Harvey Tp., 11 Jul 1974, *Catling & McKay s.n.* (CAN, TRT); 1.79 air mi NE of Nogies Creek, 1.1 air mi NNW of jct. of Co. Rd. 36 and Quarry Rd., 0.37 road mi NW from jct. of Quarry Rd. and Ledge Rd., 18 Jun 2005, *Estes 07955* (CAN, DAO, NY, MICH, TENN, VDB). **Prince Edward Co.:** Big Sand Bay, Long Point, 7 Jun 1963, *Brassard & Hainault 2702* (CAN*, TRT); ca. 2 mi SE of Milford, 5 Aug 1951, *Soper & Heimburger 5412* (TRT); South Marysburgh Township, Hilltop Rd., ca. 5 km SE of Milford, near South Bay, 19 Jun 2006, *Oldham 32786* (DAO, MICH, MO, NHIC, NY, TENN, TRT, US).

U.S.A. ALABAMA. Franklin Co.: ca. 5–6 mi E of Russellville along N side of New Hwy 24, just W of jct. of New Hwy 24 and County Rd. 83, 15 May 2003, *Estes 04625* (TENN). **Lawrence Co.:** by Ala. 36 ca. 2 mi. e. jct. Ala. 157, 6 May 1978, *Kral 61662* (JSU, VDB*); approx. 4 mi NW of Mt Hope, ca. 1.5–2 mi E of Franklin County line, W of Town Creek, at Prairie Grove Glades preserve, 15 May 2003, *Estes 04611* (TENN†); ca. 0.2 to 0.4 mi ESE of Landersville, south of junction of Hwy 24 and County Rd. 55, growing in wet ditch over limestone on west side of County Rd. 55, 34°28'09" N, 87°23'46"W, 29 Apr 2004, *Estes 05928* with *Webb* (CAN, MO, TENN, UNA). **Morgan Co.:** 5.6 mi. W of Falkville, 23 Apr 1968, *Kral 30494 B* (GA, VDB*); seep in sandy clay field 1 mi E jct AL 157 by AL 36, W of Danville, 14 Apr 1978, *Kral 61500* (JSU, MO, VDB); N side of Morgan Co Rd 55, 0.9 mi E of Massey (McKendree Church),

2.1 mi W of Lebanon Church and 6 mi W of int. US 31 at Falkville, 28 Apr 1989, *Orzell & Bridges 9380* (TEX*). **ILLINOIS. Will Co.:** Romeo, 18 Jun 1898, *Umbach s.n.* (US). **TENNESSEE. Bedford Co.:** N side Deason by US 231, 28 Apr 1974, *Kral 52571* (MO, VDB); 0.2 mi N of US 41A at Rover along Bunker Hill Rd, 3 Jun 1993, *Kral 82558 with Rust* (VDB); approx. 5 mi NE of Unionville, ca. 0.75 mile S of Newtown, near intersection of Longview Rd. and Putnam Well Rd., on east side of Longview Rd., 22 May 2003, *Estes 04583 with Wofford et al.* (CAN, GH, TENN†). **Cannon Co.:** by US 71S, 0.5 mi E of Readyville, 20 May 1974, *Kral 52812* (MO, VDB*). **Coffee Co.:** Manchester prairie, 4 mi E of Manchester on US 41, 7 Jun 1966, *Baskin & Caudle 258* (VDB). **Davidson Co.:** Hamilton Creek Recreation Area, SE side of Nashville, W of Percy Priest Lake, E side of Ned Shelton Rd., 15 Jun 2003, *Estes 04894* (EKY, GA, JSU, TENN*, UNA). **Giles Co.:** S of Pulaski, Cedar Grove community, growing on W side of Hwy 166, south of Everly Branch and just N of Cedar Grove Church, 18 Apr 2003, *Estes 04454* (TENN*). **Marshall Co.:** 2.1 mi ESE Pottsville on TN 99, 2 Jun 1969, *Kral 34776* (MO, VDB*); N side TN 99, just inside W county border, 14 May 1988, *Kral & Kral 74722* (VDB); approx. 4 mi NE of Chapel Hill near Beasley community, ca. 100–200 yards east of intersection of Hwy 99 and Beasley Rd., S side of Beasley Rd., 22 May 2003, *Estes 04582 with Wofford et al.* (GH, MO, NCU, NY, TENN†, TEX, UC). **Maury Co.:** ca. 2 mi NW of Pottsville, 1.5 mi NE of jct of Hwy 412 and Rally Hill Rd., E side of Rally Hill Rd., 22 May 2003, *Estes 04672 with Wofford et al.* (TENN†). **Rutherford Co.:** 10 mi. E Beech Grove along US 41, 9 Jun 1970, *Kral 26889* (FSU*, SMU, TENN, VDB); SE of Eagleville, 1 mile off S.R. 99, 28 May 1996, *Rust 66* (VDB*); WSW of Fosterville, ca. 2 mi W of US Hwy 231, 0.33 mi N of Squire Hall Rd., E side of Harrison Rd., 22 May 2003, *Estes 04586 with Wofford et al.* (NCU, TENN†, VDB); E of Murfreesboro, approx. 1 mi SE of Halls Hill Pike, S side of Factory Rd., Flat Rock Cedar Glade and Barrens State Natural Area, 22 May 2002, *Estes 03337* (TENN*); approx. 4 mi E of Murfeesboro on Hall Hill Pike, turn S onto Smith Hall Rd. (a dead-end road), E side of road, 22 May 2002, *Estes 03336* (TENN*); N Murfeesboro, ca. 1 mile W of intersection of E Northfield Blvd. and Hwy 96, 22 May 2003, *Estes 04574 with Wofford et al* (TENN*); approx. 4–5 mi E of Murfreesboro, W side of Factory Rd., Flatrock Cedar Glades/Barrens State Natural Area, 1 May 2003, *Walck s.n.* (TENN*); base of Garrett Knob, 29 May 2003, *Bailey & Lincicome s.n.* (TENN). **Wilson Co.:** Lebanon, 2 Jun 1923, *Pennell 11377* (PH); Cedars of Lebanon State Forest and Natural Area, N of Moccasin Rd. / Proctor Trail, 8 May 2003, *Bailey s.n.* (TENN). **TEXAS. Bell Co.:** 6 mi SE of Belton, *Wolff 2317* (SMU). **Llano Co.:** Llano River east of Packsaddle Mountain, 4 May 1947, *Whitehouse 18477* (SMU, UC, US). **Williamson Co.:** Round Rock, 24 March 1890, *Bodin s.n.* (PH, MIN-digital image); ca. 3.9 mi SSW of Liberty Hill, along CR 284, 1.3 mi W of jct CR 282, S side rd, 29 Apr 2005, *Turner & Turner 122* (BRIT, MO, TENN, TEX); southern part of co., just NW of Round Rock, FM 1431 at jct Sam Bass Rd., SE corner, 150 m S of FM 1431, 29 Apr 2005, *Turner & Turner 119* (BRIT, GH, MO, TENN, TEX).

Gratiola graniticola D. Estes, sp. nov. (**Fig. 9**). TYPE: U.S.A. GEORGIA. DeKalb Co.: Rock Chapel, GA hwy 124 at Rock Chapel County Park, gneiss flatrock, W side of highway, vernal pools, 2 May 1984, *Allison 2101* (HOLOTYPE: GA).

Gratiola graniticola a *G. neglecta* Torr. differt herba trichomatibus brevioribus basi bulbosis vestita; caulibus gracilioribus, simplicibus vel infrequenter ramosis; foliis brevioribus angustioribusque, lanceolato-ovatis vel anguste oblongis, marginibus subintegris vel inconspicue dentatis, basibus magis valde amplectentibus; pedicellis folia bractealia subtendentia aequantibus vel eos duplo longioribus; bracteolis calycibus brevioribus vel eis vix superantibus; floribus minoribus lobis posterioribus purpurascentibus, barba in corollae orificio e trichomatibus albidis translucentibusve constante; capsulis minoribus, magis subglobosis purpura suffusis; seminibus minoribus magis obscure cinereis.

Plants annual, solitary, erect herbs, (7–)9–21(–29) cm tall. Root simple, fleshy, whitish with numerous rootlets. Stems erect, somewhat fleshy, simple or with few ascending branches, terete or slightly rounded-quadrangular in cross section, (0.7–)0.9–1.2(–1.5) mm in diameter at midstem; with (6–)7–10(–12) leafy nodes, mid-internodes (15–)17–30(–36) mm long, basal internodes shortened (1.5–8 mm); green or suffused with reddish or reddish-pink pigments, especially near the base and upper nodes; glabrous or glabrate near base becoming increasingly pubescent upward, with spreading, translucent, conical or bulbous-based, glandular trichomes. Leaves simple, oppositely decussate, similar in shape but gradually reduced in size from base to apex, lowermost often congested due to the shortened internodes and sometimes early deciduous, lanceolate-ovate to narrowly oblong usually widest at or below the middle, horizontally spreading with tips curved upward, with one evident main vein or trinerved with two short secondary veins, slightly fleshy-thickened, blades (6–)7–13(–18) mm long and 1–3(–5) mm wide, (2.8–)3.5–5.7(–7.4) times longer than wide, apex narrowly obtuse, margins entire or with 1–2(–3) pairs of remote, low, bluntly pointed teeth beyond the middle, base usually amplexicaulate; blades green or leaf tips, teeth, and basal leaves often suffused with reddish pigments; proximal leaves glabrate, median and distal leaves moderately pubescent with bulbous based trichomes. Flowers solitary in axils of upper bracteal leaves, erect to spreading, zygomorphic, perfect; pedicels slender, ascending, (5–)8–17(–22) mm long, (0.9–)1–2(–2.3) times as long as the subtending bracteal leaves, sparsely to moderately pubescent with bulbous based trichomes. Bracteoles 2, paired, closely subtending the calyx, usually shorter than or equaling the sepals, lanceolate and often falcate, longitudinally 3-nerved (sometimes single nerved) though not often evident when fresh, fleshy-thickened, 2–4.5 mm long and 0.5–1.0 mm wide,

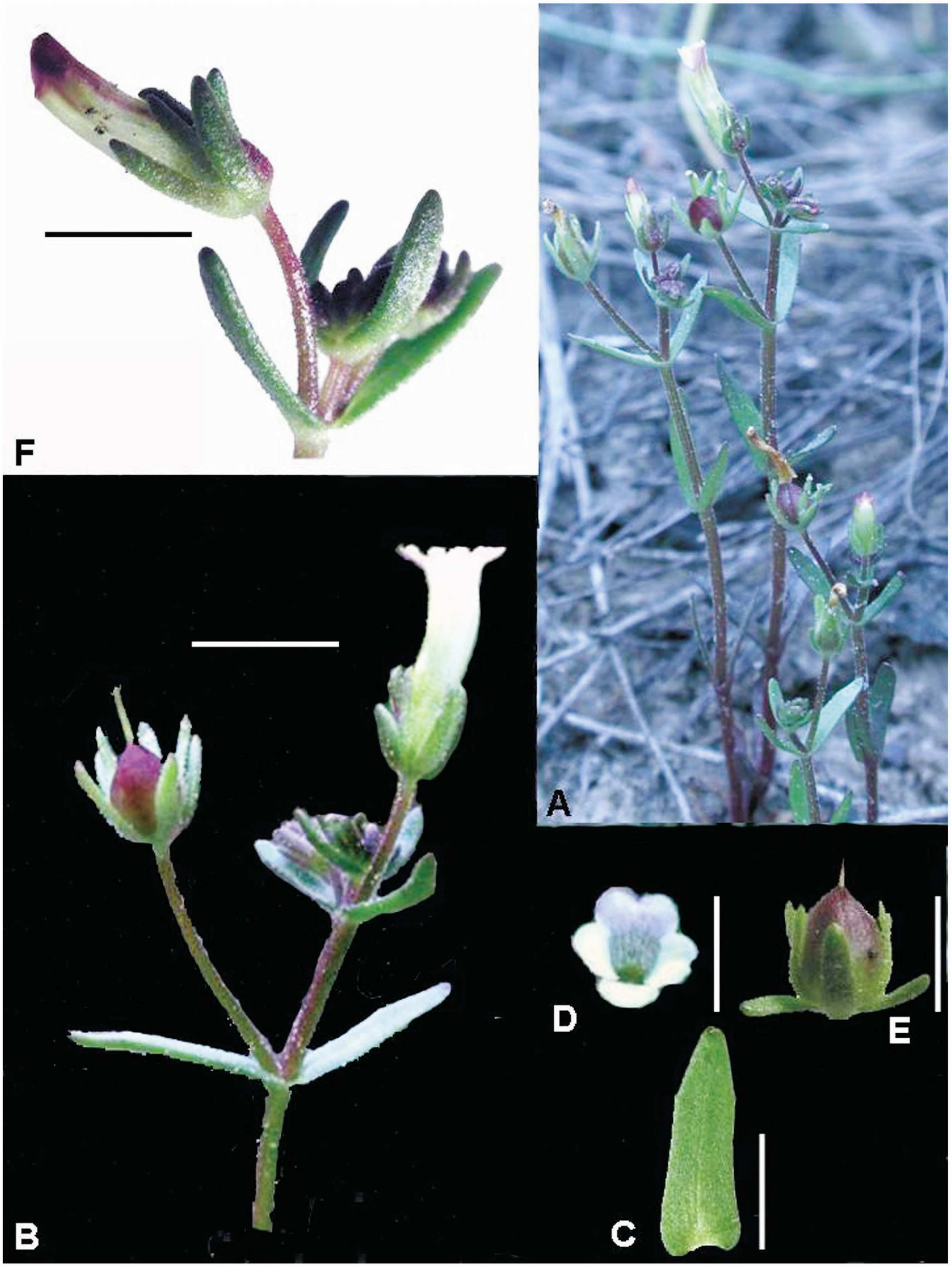

Fig. 9. *Gratiola graniticola*. **A.** Habit, in Butts Co., Georgia, 10 Apr 2004. **B.** Upper stem with flower and immature capsule (scale bar = 6 mm). **C.** Leaf (scale bar = 5 mm). **D.** Flower, front-view (scale bar = 2 mm). **E.** Immature capsule with subtending calyx and bracteoles (scale bar = 3.5 mm). **F.** Unopened flower showing purplish corolla lobes (scale bar = 4.5 mm).

apex obtuse, margins entire, surface green, apex purple-tipped, abaxial surface convex, moderately covered on both surfaces with bulbous-based trichomes. Calyx irregularly campanulate with 5 subequal, distinct, lanceolate sepals, longitudinally 3-nerved (sometimes single nerved) though not often evident when fresh, fleshy-thickened, green on the surface with a minute purple tip, 2–4.2 mm long and 0.5–1.3 mm wide, apex obtuse, margins entire, moderately covered, especially abaxially, with conical or bulbous-based trichomes. Corolla tubular-funnelform, gamopetalous, slightly marcescent, and zygomorphic, 6.8–9.0 mm long; corolla tube quadrangular, dorsal surface with a hump near midpoint, 5.5–6.8 mm long and 1.3–1.9 mm in diameter, outer surface pale yellowish-green or cream-colored, often purplish or pinkish dorsally, faintly to conspicuously purple-lined exteriorly, scarcely pubescent with conical or bulbous-based trichomes, inner surface near orifice at base of posterior corolla lobe with sparse beard of clavately thickened whitish to translucent trichomes, proximal and middle inner corolla surfaces pilose with eglandular trichomes; corolla lobes 5, each usually broader than high and often emarginated at apex, spreading, the lower three white or cream-colored, the upper two strongly suffused with purple or pink, the lobes 1.0–1.7 mm high and 1.5–2.3 mm wide, adaxial surfaces glabrous, abaxial surfaces glabrous. Stamens 2, inserted near the middle of the dorsal surface of the corolla tube, filaments to 1.2 mm long, anthers transversely oriented to the filament, 0.5–0.7 mm long and 0.5–0.6 mm wide, connective greatly dilated around the two anther sacs, whitish; staminodes inserted ca. 1–1.3 mm from base of corolla tube or absent, when present minute and ca. 0.2 mm long, not capitate. Gynoecium 4.4–4.8 mm long, subtended at the base by an orange nectary ring, ovary 1.6–2.0 mm long and 1.2–1.7 mm in diameter, style 1.9–2.2 mm long, stigma 2-lobed, dilated and flattened, 0.5–0.6 mm long. Capsules subglobose to slightly ovoid, (2.4–)2.8–3.6 mm long, 2.1–3.7 mm in diameter, purple tinged when mature. Seeds several hundred per capsule, brown to grayish-brown, 10–13 ribbed, longitudinal ridges more conspicuous than the transverse ridges, asymmetrically ovoid to short cylindric, often oblique at one end, surface reticulate with rectangular alveolae, alveolae covered by a thin iridescent membrane, (0.3–)0.36–0.42(–0.47) mm long and (0.17–)0.2–0.24(–0.27) mm wide, (1.3–)1.6–2.1(–2.5) times longer than wide. Chromosome number unknown.

Phenology.—Flowering and fruiting from April to May.

Etymology.—The ephithet *graniticola* was chosen to reflect the granite flatrocks that this species inhabits.

Common Name.—Granite hedge-hyssop.

History of Taxon.—*Gratiola graniticola* was apparently first collected in 1928 (*Wherry & Benedict s.n.* PH) from "pools on granite ledges" in Gwinnett County, Georgia. A decade later, Pyron and McVaugh (*2866* GA, PH), collected a specimen of *G. graniticola* from granitic areas in Oglethorpe County, Georgia. McVaugh sent a specimen of this Oglethorpe County collection to F.W. Pennell who wrote "your collection, with that of Wherry and Benedict…differ from *G. neglecta* Torr. by bracts shorter relative to pedicels, capsules smaller (3 mm long), upper corolla-lobes purple or purplish, and seeds smaller and grayer" (McVaugh 1943). He added that these specimens seemed to match his description and photograph of *G. gracilis* Benth., a species described by Bentham (1846) from Texas.

Bentham (1846) described *G. gracilis* Benth. from material collected by Drummond near Harrisburgh, Texas (near present-day Houston) in ca. 1834. Unfortunately, Drummond failed to note the habitat from which he collected the plants. A second specimen annotated by Pennell as *G. gracilis* was collected by Lindheimer (*43* MO) from nearby Galveston in ca. March (May?, illegible) 1842. Like Drummond, Lindheimer did not provide specific locality or habitat information. Despite being known only from herbarium specimens, *G. gracilis* was maintained as a species by Small (1903) and Pennell (1921). Later, Pennell (1935) reduced *G. gracilis* to synonymy with *G. neglecta* noting the characters Bentham used to distinguish *G. gracilis* from *G. neglecta* "are all variable features that occur without geographic correlation."

During this study, a photograph of the holotype of *G. gracilis* (*Drummond coll. 3, n. 284*, K) and an isotype (GH) were examined. As Pennell noted, these specimens do share some features with those plants from the Georgia granite outcrops, most notably in the length of the leaves and the ratio of the length of the pedicel and subtending bract. While of rare occurrence, *G. neglecta* can have relatively short leaves and bracteal

leaves shorter than the pedicels (e.g., *Guthrie 1002* VDB, Lake Co., TN). The three *G. gracilis* specimens also differ from *G. graniticola* in that they lack purple coloration on the corollas and capsules, features diagnostic for *G. graniticola*. In terms of habit, the stems of the *G. gracilis* specimens are more branched like those of *G. neglecta* compared to those of *G. graniticola*, which are mostly simple. Lastly, *G. graniticola* is endemic to granite outcrops and has not been found in non-granitic areas. Since there are no granite outcrops in southeastern Texas, it is reasonable to assume that the plants collected by Drummond and Lindheimer likely came from a different habitat type. Based on the evidence presented above, we follow Pennell and recognize *G. gracilis* as a synonym of *G. neglecta*.

Conservation Status.—*Gratiola graniticola* should be considered a rare species in Georgia due to the small number of populations and limited distribution.

Representative Specimens Examined.—**U.S.A. GEORGIA. Barrow Co.:** Winder, GA Hwy 81, roughly 0.25 mi S of junction with US Hwy 29, E side of highway, 30 Apr 1984, *Allison 2095* (GA*); same site, 19 May 2003, *Estes 04590 with Allison* (TENN*†). **Butts Co.:** ca. 2.7 mi NNE of Jackson, GA Hwy 36, ca. 0.5 mi S of Cedar Rock Church, E side of highway, 13 May 1984, *Allison 2175* (GA*); same site, 10 Apr 2004, *Estes 05742* (TENN). **Columbia Co.:** ca. 4.25 mi ESE of Appling, ca. 0.45 mi NNW of confluence of Little Kiokee Creek and Benton Branch, adjacent to Heggies Rock Preserve, 10 May 1987, *Allison 2842* (GA*). **DeKalb Co.:** across from Rock Chapel Park, 4 mi N of railroad track in Lithonia, along State Hwy 124, 16 Apr 1978, *Patrick 592 with Wofford et al.* (TENN*); Lithonia, ca. 0.3 mi N of intersection of Interstate 20 and Hwy 124, NW side of the intersection of Hwy 124 and Conyers Street on small concealed granite outcrop, 10 Apr 2004, *Estes 05733* (TENN); same site as previous, 01 May 2004, *Estes 05954* (TENN*, MO, NY). **Greene Co.:** 8.2 mi SSE of Greensboro, 5.8 mi W of White Plains, 2 May 1987, *Allison 2834* (GA*); ca. 9 mi SSE of Greensboro, ca. 1.5 mi SW of Mosquito Crossing, S side of Leach Flatrock Rd., 33.46738 N, 83.13214 W, 19 May 2003, *Estes 04585 with Allison* (NCU, TENN†). **Gwinnett Co.:** 6 mi SW of Grayson, 3 May 1928, *Wherry & Benedict s.n.* (PH); 4.25 mi E of Snellville, 2.25 mi SSE of Grayson, Langley Rd., 0.34 mi by air NW of junction with US Hwy 78, E side of road, 13 Jun 1984, *Allison 2306* (GA). **Hancock Co.:** 3.5 mi SE of Sparta, 11 May 1952, *Duncan 13533* (GA, digital image); ca. 1 mi or less NE of Sparta, 0.3 mi N of Hwy 16, 0.3 mi W of Twomile Creek, 33.29098 N, 82.95428 W, *Estes 04659 with Allison* (TENN*). **Hart Co.:** 5.3 mi NNE of Vanna, 1.5 mi NNE of Goldmine, ca. 0.2 mi E of county road 141 at a point ca. 0.45 mi NW of junction with county road 140, 15 Apr 1986, *Allison 2625* (GA*); same site, 19 May 2003, *Estes 04588 with Allison* (NCU, TENN†). **Newton Co.:** ca. 3 mi NE of Covington, ca. 1.25 mi NE of the intersection of Hwy 142 and Alcovy Rd., S side of Alcovy Rd., 19 May 2003, *Estes 04584 and Allison* (TENN†); same site, 10 Apr 2004; *Estes 05738* (TENN). **Oglethorpe Co.:** Echols' Mill, May 1938, *Pyron & McVaugh 2866* (GA, PH); ca. 0.5 mi E of Echols' Mill, ca. 9.3 mi N 45 deg. of Lexington, 7 May 1978, *Treiber & Nesom 1518* (NCU*). **Pike Co.:** 1.6 mi S of Hollonville on Concord Road, E side of road, 19 May 1984, *Allison 2254* (GA*); same site, 01 May 2004, *Estes 05953* (MO, NY, TENN). **Upson Co.:** NE corner of county, ca. 0.4 mi S of Lamar County line and just E of Barnesville-Yatesville Rd., 18 May 1984, *Allison 2235* (GA*). **Walton Co.:** 4.9 mi WNW of Walnut Grove, Ace Moon Road (county road 197), just S of junction with Sharon Church Road (county road 106), E side of road, 11 May 1984, *Allison 2141* (GA*); by GA 138, 1 mi. NE of Walnut Grove, 17 May 1989, *Kral 72517* (FSU, GH, VDB*).

ACKNOWLEDGMENTS

We appreciate the work of two anonymous reviewers whose suggestions improved this manuscript. Funding for this research was provided by three University of Tennessee endowment funds, the Breedlove-Dennis Fund, the Sharp Fund, and the Hesler Fund. Additional funding was received from the Southern Appalachian Botanical Society (Core Award) and a University of Tennessee Department of Ecology and Evolutionary Biology summer research grant. Gene Wofford, Ron Petersen, Ken McFarland, Jeff Walck, Kurt Blum, John Beck, and Ed Lickey provided advice or encouragement. We are also grateful to the following individuals who assisted with field work or specimen collection: Jim Allison, Matt Turner, Billie Turner, Bill Carr, John Beck, David Webb, Michael Oldham, Eric Ulazsek, Steve Hill, Claude Bailey, Roger McCoy, and David Lincicome. John Dunlap assisted with the SEM work. Chris Fleming assisted in the preparation of the species distribution maps. Mark Garland prepared the Latin diagnoses. We also wish to thank the curators of the herbaria that loaned specimens for this study, facilitated herbarium visits, or provided us with digital images of specimens.

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